

Quantifying Trophic and Demographic Rates of Plankton-Rich Layers in East Sound, Orcas Island, Washington

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LONG-TERM GOALS

Localized concentrations of plankton (i.e. patches) alter the optical and acoustical properties of the water column and can have significant ramifications for the ecological dynamics of marine communities. The goal of this research is to develop a mechanistic understanding and predictive capability of the biological drivers of plankton patch formation, persistence and decline. This goal will be addressed by concurrent characterization of the physical, chemical and biological parameters associated with patch occurrence and dissipation with biologically meaningful resolution (meters and days).

OBJECTIVES

The objective of the funded work is to quantify the contribution of ecological processes to plankton patch formation in the coastal ocean. These objectives will be addressed by simultaneously quantify (1) spatial and temporal characteristics of large plankton patches, (2) the physical and chemical conditions these patches occur in and (3) the plankton population dynamics of the dominant layer forming species through simultaneous measurements of their growth and mortality rates.

APPROACH

The methodological approach of this research is to concurrently quantify the population dynamics of whole plankton communities and the environmental conditions they occur in. Frequent, small boat surveys allow us to characterize physical water column structure and capture discrete samples to measure nutrient, plankton biomass and Chl *a* concentrations as well as laboratory measurements of plankton growth and grazing rates. This research utilizes methods widely used in biological oceanography as well as more recent approaches established and tested during my work in East Sound. Some of the results have recently been published (Menden-Deuer, 2008).

Small boat surveys, East Sound, Orcas Island

East Sound is a temperate fjord within the San Juan Archipelago in the Northeastern Pacific (N 48° 39', W 122° 53', Figure 1). The fjord has a north-south extent of approximately 9 km, an east-west width of 1 - 2 km and mean depth of 30 m. Circulation and exchange with the tidally well-mixed water

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outside is restricted by a partial sill at the southwestern terminus of the fjord. Previous, ONR funded work, has established East Sound, Washington as a site of recurring plankton layer presence and provided great insight into the physical forcing mechanisms (Dekshenieks et al. 2001). The presence of distinct plankton layers was subsequently confirmed in a variety of coastal environments, highlighting that layers are a common rather than rare occurrence (McManus et al. 2005). From our land base, at the Shannon Point Marine Center, part of Western Washington University, East Sound is easily accessible by small boat within 30 - 45 minutes. Previous work has established that plankton layers in East Sound are continuous and coherent structures on a daily basis, but that significant changes in the composition occurs on the order of a few days (Menden-Deuer, 2008). Based on these findings, our small boat surveys were carried out on alternating days. A total of four to five stations were sampled on each day, with four stations located within East Sound and a reference station outside the sound, where no layers have been observed (Fig. 1). In addition, an additional 11 stations were sampled on July 28th 2008 during the occurrence of an intense diatom layer in the northern section of East Sound (Fig. 1 inset). The goal of this sampling scheme was to increase spatial resolution and determine the edge of layer extent. Layer presence was determined by profiling the water column with a SeaBird 19+ CTD (T, S, P, σ_t) and auxiliary fluorometer (Wetlabs WetStar). Layers were sampled during the summer at intervals of 1-3 days for a total of 2-3 weeks, to relate short-term changes (among days) in layer characteristics to longer-term changes (among weeks). By conducting this work over several days, predictions of changes in plankton layer intensity will be comparable to subsequent, observed plankton rich layer (PRL) intensities. Water samples from within PRLs and surrounding waters were collected with a 2L and 10L horizontally-mounted Niskin bottle.

Biological quantities and rate measurements

At the laboratory, water samples from all stations and all depths are analyzed for extracted Chl *a* and nutrient (phosphate, nitrate and silicate) concentrations. Whole water samples are preserved with Lugol's iodine to a final concentration of 2% (Menden-Deuer et al. 2001) for taxonomic analysis. These measurements help place the field and rate measurement data in a quantitative, biological context. To establish the rates of change of plankton three different methods are used in the course of this field work, two independent methods to measure primary productivity and the dilution method to measure zooplankton grazing impact. In combination, these methods quantify both the potential for plankton layer occurrence as well as dissipation due to biological processes. In the context of the physical, chemical and biological observations outlined above, they provide a synoptic picture of the factors controlling plankton biomass: standing stock, available nutrients, grazer induced mortality and environmental structure and stability.

The rate of change in phytoplankton biomass is measured using the radio-labeling method that was first developed by Steemann Nielsen (1952) to quantify photosynthesis. Since its invention, the method has been effectively applied to measure phototrophic processes, including phytoplankton growth rates, carbon to *Chl a* ratios (Welschmeyer & Lorenzen, 1984), heterotrophic protist grazing rates (Montagnes & Lessard, 1999), and cellular carbon content (Putt & Stoecker 1989, Crawford & Stoecker 1996, Menden-Deuer & Lessard 2000). The radio-labeling technique exploits the fact that photosynthetic organisms incorporate inorganic CO₂ to generate their tissue and measurements with a scintillation counter are sensitive enough to detect ¹⁴CO₂ within a single cell (e.g. Menden-Deuer & Lessard 2000). A known fraction of the total CO₂ is offered as a radio-labeled tracer (¹⁴CO₂). The uptake rate of the tracer can then be used to calculate photosynthetic rates. In this project, the radio-labeling method was used in two variations:

First, standard primary productivity experiments were run under in-situ conditions by incubating radio-labeled samples in an incubator that is cooled with ambient seawater and exposed to ambient surface light. The light levels of the incubations span the range of light levels observed in the field. Light levels are adjusted using neutral density screen, resulting in typically 6 independent incubations, per station and depth, without replication. Samples are incubated for 2 hrs on a rotating wheel to ensure mixing of the contents. The experiments are terminated by filtering of the samples and acidification. Incorporation of radio-active isotope is measured using a standard scintillation counter. Measures of decays per minute are converted to Chl *a* and C specific production rates.

The second type of primary productivity experiment was conducted in a controlled light box, with positions that correspond to known light levels. This approach allows much greater replication, and in these experiments, 14 light levels were used to estimate the rate of photosynthetic activity and capacity. The advantage of this experimental approach is the much greater replication as well as estimation of photosynthetic potential. The disadvantage is that the incubation corresponds less to in-situ conditions than the method outlined above. To offset this disadvantage, we designed the light levels such, that they would span the range of intensities plankton would experience in summer in the coastal, temperate ocean. During incubation, samples are cooled to ambient water temperatures. During 2008, I tested a variation of this method that adds incubations of diluted seawater samples, to test whether a combination of the dilution and primary productivity methods is possible. This approach is described in more detail under ‘work completed’.

The dilution method (Landry and Hassett 1982) is used to complete the assessment of biological processes that alter plankton standing stock and productivity. Specifically, it was used to assess potential loss of phytoplankton due to grazing mortality and subsequent increases in zooplankton due to growth. The dilution experiments were conducted according to protocols established by Suzanne Strom (WWU) and her laboratory. Whole water samples were prescreened through a 200 μm mesh, so that larger zooplankton were eliminated from the experiments, to avoid grazing of copepods on the microzooplankton predators. Two dilution levels (5 and 100%) were run in triplicate, some experiments had an additional, nutrient-addition treatment to avoid nutrient limitation of the primary producers. All samples were incubated for 24 hrs, cooled with ambient seawater and exposed to ambient surface light levels. Light levels were adjusted to the sample depth with neutral density screen.

This work builds upon prior ONR funded work in East Sound conducted by, incomplete, in alphabetical order: Alldredge, Cowles, Donaghay, Grünbaum, Holliday, McManus, Perry, and Zaneveld. This project was conducted simultaneously, and in collaboration with Tatiana Rynearson investigating how genetic diversity affects the development and persistence of plankton layers.

WORK COMPLETED

Field-work was conducted between July 9th and August 4th 2008. A total of 9 day cruises to East Sound, Orcas Island were undertaken from the land base of Shannon Point Marine Center, Anacortes, Washington. During a typical cruise, a total of four stations were visited, three within East Sound and one reference station outside the sound; to increase spatial resolution, a sampling grid of 11 additional stations was sampled in the northern half of East Sound (Fig. 1, inset). To increase temporal resolution, some stations were sampled repeatedly over the course of a few hours. At each station, a vertical profile of the physical properties of the water column as well as phytoplankton fluorescence were recorded with a SeaBird CTD 19. In addition, in 2008 light intensity and particle abundance were

measured using a Biospherical QSP-2300L Quantum Scalar (4 pi) PAR sensor and a WET Labs C-Star transmissometer respectively. Except for the transmissometer, which has a path lengths of 25 cm, the vertical resolution was approximately 0.2 m. Discovery of layer presence and distribution was possible through real time acquisition of fluorescence data. The CTD mounted fluorometer has been calibrated for different plankton communities in East Sound for 4 years now and is considered a reliable indicator of phytoplankton biomass. Two target depth were sampled at each station, with depths and volume captured depending on layer location and planned analyses. On all days, at all stations, water samples were collected to preserve whole water samples for taxonomic analysis, a size fractionated, triplicate Chl *a* analysis (> and <20 μm) as well as analysis of dissolved inorganic nutrients (phosphate, nitrates and silicates). In total, over 500 Chl *a* samples were taken, 83 nutrient samples were analyzed for dissolved phosphate, nitrate and silicate concentrations as well as 20 samples preserved for taxonomic identification of the major plankton species in the size range of 5 to 200 μm .

The effort necessary to conduct growth and grazing rate measurements is immense and typically results in a coarse resolution of the underlying biological dynamics. Thus, in 2008, I added a focus on both getting quantitative rate measurement data on plankton growth and mortality and improving the methodology to reduce sampling effort and increase sampling resolution. The new method I am trying to develop aims to combine the information gained from dilution experiments with the high-sensitivity of radio-isotope labeling. Whole seawater samples were incubated with the addition of trace amounts of radioactive bi-carbonate. Samples were incubated at constant temperature (12 C) and a standardized range of 14 light levels in 20 ml glass scintillation vials. When whole seawater samples are incubated, the experiment is identical to a classic P vs E (photosynthesis vs. irradiance) measurement and yields parameters of photosynthetic performance. In addition, I prepared samples at a range of dilutions of whole seawater (0.1, 0.4, 0.75), following the dilution experiment protocol (Landry & Hassett, 1982), which assumes that with increased dilution, predator prey encounter rates decrease, thus grazer induced mortality is sequentially lowered until only (theoretically) phytoplankton growth is measured. Thus, I am aiming to combine these two experimental approaches to yield a method that quantifies ecologically relevant rates at the necessary resolution. Primary productivity experiments under simulated conditions, in temperature controlled light boxes at 14 light levels were conducted on 5 different cruise days, two of which included the dilution approach described above. These types of primary productivity experiments were run using variations in size fractionation and time-course experiments to decipher the particular effect these factors have on the resulting measurements.

Finally, two guest investigators joined me during the 2008 field season. Laurent Seuront (Flinders University, Australia) tested the performance of a high-resolution (512 Hz) fluorometer alongside our investigation using a free-falling profiler. Justin Seymour (MIT) quantified the occurrence of heterotrophic bacteria in association with plankton rich layers using fluorescent in situ hybridization and flow cytometry. In addition, he collected measurements of respiration rates of heterotrophic bacteria.

RESULTS

The intensive sampling effort undertaken to quantify the biological dynamics of plankton rich layers in East Sound, Washington within a physical and chemical context revealed a rich and dynamic picture of the interplay between physical forcing and biological response. Specifically, over the course of now two seasons, our results provide multiple examples of plankton patch formation, persistence and decline in their physical context. Having gathered data with daily and meter-scale resolution provides an exciting opportunity to extrapolate biologically relevant small-scale processes to scales relevant to

the optical and acoustical properties of the water column. Since the fieldwork only ended last month, the results presented for 2008 are only a fraction of the total data acquired. Results from the 2007 season are not repeated here, due to space limitation.

Over the three-week period, we observed two distinct layer formation events (Figures 2 and 3). The first observed plankton rich layer was a subsurface maximum at around 5 m depth dominated by a $<10\ \mu\text{m}$ motile autotrophic prasinophyte, (*Pyramimonas* sp.). The event lasted about 4 days at the southern end of East Sound and 7 days at the northern and coincided within a salinity minimum (28 PSU). The second plankton patch consisted of the diatoms *Coscinodiscus* sp. and *Pseudo-nitzschia* spp.) and was associated with a distinct pycnocline, although stratification was observed in the previous week, without the concurrent presence of a plankton layer.

These field observations were amended with direct sampling of the layer structures and surrounding waters with respect to Chl *a* concentrations, species composition, nutrient availability and the respective growth and grazing rates measured on whole plankton communities. Chl *a* concentrations were highly variable among sampling days and stations. The highest concentrations were observed at station PRL 4 during the two plankton-rich layer events; July 14th and July 30th, 15 and 20 $\mu\text{g Chl } a\ 1\text{-l}$ respectively (Fig. 4). The precision of the Chl *a* measurements is $\sim 10\%$. Chl *a* concentrations were measured in conjunction with observations of the taxonomy and species composition of the dominant phytoplankton species. As observed in 2007, shifts in plankton community composition were observable in concurrent shifts in size-fractionated Chl *a* (Fig. 5). Analysis of nutrient concentrations showed that the water column was severely nutrient limited with respect to nitrate and to a lesser degree to phosphorous; silicate was abundant in excess relative to Redfield ratio concentrations (Fig. 6). This may explain the low abundance of phytoplankton for some of the time period. Clearly, intrusion of nutrient rich water is essential to the formation and maintenance of plankton rich layers in East Sound. For samples associated with distinct plankton patches, as well as in periods in between patch occurrence we conducted photosynthesis rate measurements and performed non-linear regression analysis of the results. The characteristic photosynthesis parameters, photosynthetic efficiency (α) and the maximum photosynthesis rate (P_{max}) were determined, alongside with their respective significance levels and probabilities. Thus, hypotheses about the relative growth potential and productivity of layer associated communities, relative to non-layer communities can be addressed. Future analyses of the association between water column structure, nutrient availability, and patch characteristics will reveal time and space scales, as well as correlations between the environmental conditions and changes in biological structure.

IMPACT/APPLICATIONS

This work characterizes the dynamics of biological patch formation and dissipation with high spatial and temporal resolution, increasing the resolution further from the 2007 season. These observations are collected within the context of detailed measurements of physical, chemical and biological parameters, including ecological rate measurements of plankton population dynamics. These concurrent measurements allow identification of the major processes and conditions under which patches form, persist and dissipate. The results of this work provide, to my knowledge, the first estimates of phytoplankton growth and zooplankton grazing rates associated with plankton-rich layers. These results provide quantitative estimates of the magnitude with which biological processes can mediate changes in the optical and acoustical properties of the water column.

RELATED PROJECTS

This work builds on previously funded ONR work in East Sound by many investigators. During the 2007 and 2008 season I worked in collaboration with Tatiana Rynearson (ONR Award N000140710912) who is investigating how genetic variation affects the development and persistence of plankton layers. Additional collaborations using the East Sound results are developing with Suzanne Strom (WWU), focusing on the occurrence of the *Heterosigma akashiwo* layer in summer 2007; with Justin Seymour (MIT), quantifying the abundance and activity of heterotrophic bacteria in association with plankton patches and Laurent Seuront (Flinders University, Australia), who is testing a high-frequency (512 Hz) free-falling fluorometer to characterize the spatial distribution of plankton patches.

REFERENCES

Crawford, D. W. and D. K. Stoecker. 1996. Carbon content, dark respiration and mortality of the mixotrophic planktonic ciliate *Strombidium capitatum*. *Marine Biology* 126: 415-422

Dekshenieks MM, PL Donaghay, JM Sullivan, JEB Rines, TR Osborn, Twardowski MS 2001 Temporal and spatial occurrence of thin phytoplankton layers in relation to physical processes. *Mar Ecol Prog Ser* 223: 61-71

Landry MR and Hassett RP 1982 Estimating the grazing impact of marine microzooplankton. *Marine Biology*, 67, 283-288

McManus, M. A., Alldredge, A. L., Barnard, A. H., Boss, E., Case, J. F., Cowles, T. J., Donaghay, P. L., Eisner, L. B., Gifford, D. J., Greenlaw, C. F., Herren, C. M., Holliday, D. V., Johnson, D., MacIntyre, S., McGehee, D. M., Osborne, T. R., Perry, M. J., Pieper, R. E., Rines, J. E. B., Smith, D. C., Sullivan, J. M., Talbot, M. K., Twardowski, M. S., Weidemann, A., and Zaneveld, J. R. 2003. Characteristics, distribution and persistence of thin layers over a 48 hour period. *Marine Ecology Progress Series* 261:1-19

Menden-Deuer S. 2008. Spatial and temporal characteristics of plankton-rich layers in a shallow, temperate fjord. *Marine Ecology Progress Series* 355: 21-30

Menden-Deuer S & EJ Lessard. 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. *Limnology and Oceanography* 45: 569-579

Menden-Deuer S, EJ Lessard & J Satterberg. 2001. Effect of preservation on dinoflagellate and diatom cell volume, and consequences for carbon biomass predictions. *Marine Ecology Progress Series* 222: 41-50

Montagnes, D. J. S. and Lessard, E. J. 1999 Population dynamics of the marine planktonic ciliate *Strombidinopsis multiauris*: its potential to control phytoplankton blooms. *Aquat. Microb. Ecol.*, 20, 167-181

Putt, M and Stoecker DK. 1989. An experimentally determined carbon: volume ratio for marine "oligotrichous" ciliates from estuarine and coastal waters. *Limnology and Oceanography* 34: 1097-1103

Steemann Nielsen, E. 1952 The use of radio-active carbon (C14) for measuring organic production in the sea. J. Cons. Perm. Int. Explor. Mer., 18, 117–140

Welschmeyer, N. A. and Lorenzen, C. J. 1984 Carbon-14 labeling of phytoplankton carbon and chlorophyll a carbon: determination of specific growth rates. Limnol. Oceanogr. 29, 135 -145

PUBLICATIONS AND PRESENTATIONS

Publications

Menden-Deuer S. 2008. Spatial and temporal characteristics of plankton-rich layers in a shallow, temperate fjord. *Marine Ecology Progress Series* 355: 21-30.

Presentations

Menden-Deuer S. 2008. Patchy prey and stealthy predators: biological drivers of planktonic food-webs. Department of Marine Sciences, University of Georgia, Athens (*invited*)

Menden-Deuer S. 2008. Patchy prey and stealthy predators: biological drivers of planktonic food-webs. School of Fisheries and Ocean Sciences, University of Alaska, Fairbanks (*invited*)

Menden-Deuer S. 2008. Plankton on the move: biological drivers of plankton predation and productivity. School of Fisheries and Ocean Sciences, University of Alaska, Fairbanks (*invited*)

Menden-Deuer S, Fredrickson KA. 2008. Biological drivers of plankton layer formation in East Sound, Orcas Island, Washington. Ocean Sciences Meeting, Orlando, Florida

Menden-Deuer S. 2008. Patchy prey & stealthy predators: integrating theory, experimentation and observation to decipher planktonic food webs. Graduate School of Oceanography, University of Rhode Island, Rhode Island (*invited*)

Menden-Deuer S. 2008. Plankton on the move: biological drivers of plankton predation and productivity. Graduate School of Oceanography, University of Rhode Island, Rhode Island (*invited*)

Menden-Deuer S. 2007. Integrating models, experiments and field observations to examine predator-prey interactions in the plankton, Estuarine Research Federation, Providence, Rhode Island

Menden-Deuer S, Fredrickson KA & Wright HA. 2007. The role of biological drivers in the formation of plankton patches. Estuarine Research Federation, Providence, Rhode Island

Menden-Deuer S & Levin SA. 2007. Linking water column structure, phytoplankton distributions and planktonic productivity: predator behaviors are a key ingredient. International Council for the Exploration of the Sea (ICES), Helsinki, Finland (*invited*)

Menden-Deuer S. 2007. Integrating models, experiments and field observations to examine predator prey interactions in the plankton. Northeast Algal Society, 46th annual symposium, Rhode Island

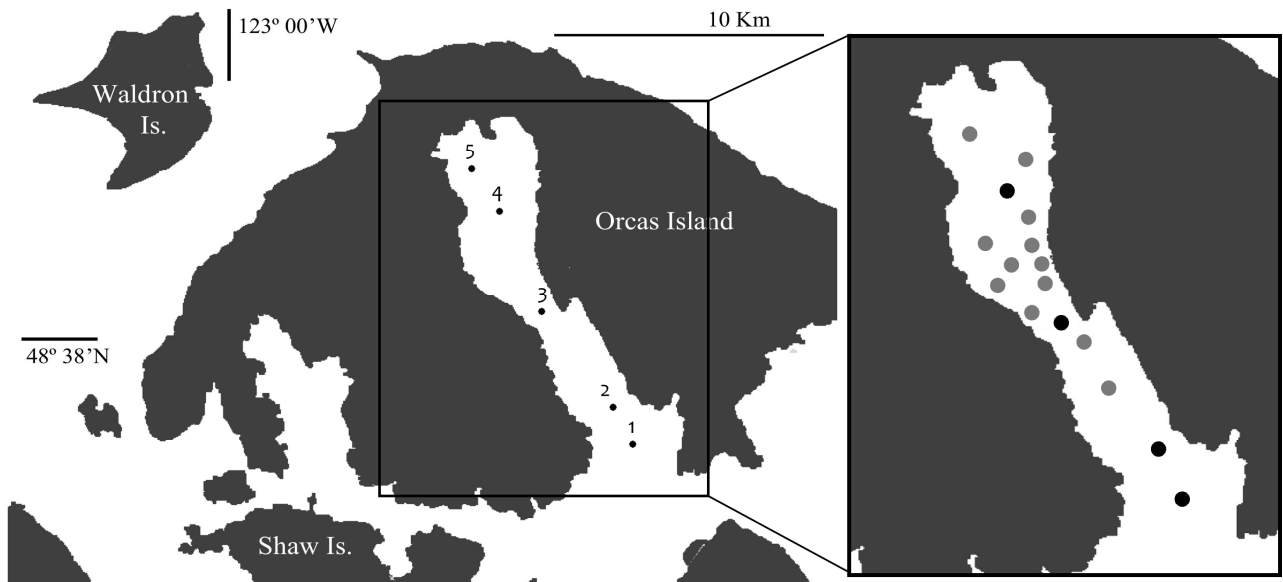
Wright H.A. and Menden-Deuer S. 2007. The role of phytoplankton productivity as a possible mechanism for plankton layer formation. Northeast Algal Society, 46th annual symposium, RI

Menden-Deuer S. 2007. Patchy prey & stealthy predators: empirical and theoretical analysis of zooplankton behaviors. Biological Sciences Colloquium Series, University of Rhode Island (*invited*)

Menden-Deuer S. 2007. One but not the same: behavioral heterogeneity is the key to predicting forager distributions when resources are patchy, Imperial College, London, UK (*invited*)

Menden-Deuer S. 2007. Patchy prey & stealthy predators: empirical and theoretical analysis of zooplankton behaviors. Woods Hole Oceanographic Institute (*invited*)

FIGURES



*Figure 1 Station locations in East Sound, Orcas Island, WA. The map shows the locations of the 5 major stations (main map) as well as the higher-resolution sampling grid (inset) visited during the occurrence of an intense diatom layer (*Coscinodiscus* sp. and *Pseudo-nitzschia* spp.) on July 28th 2008.*

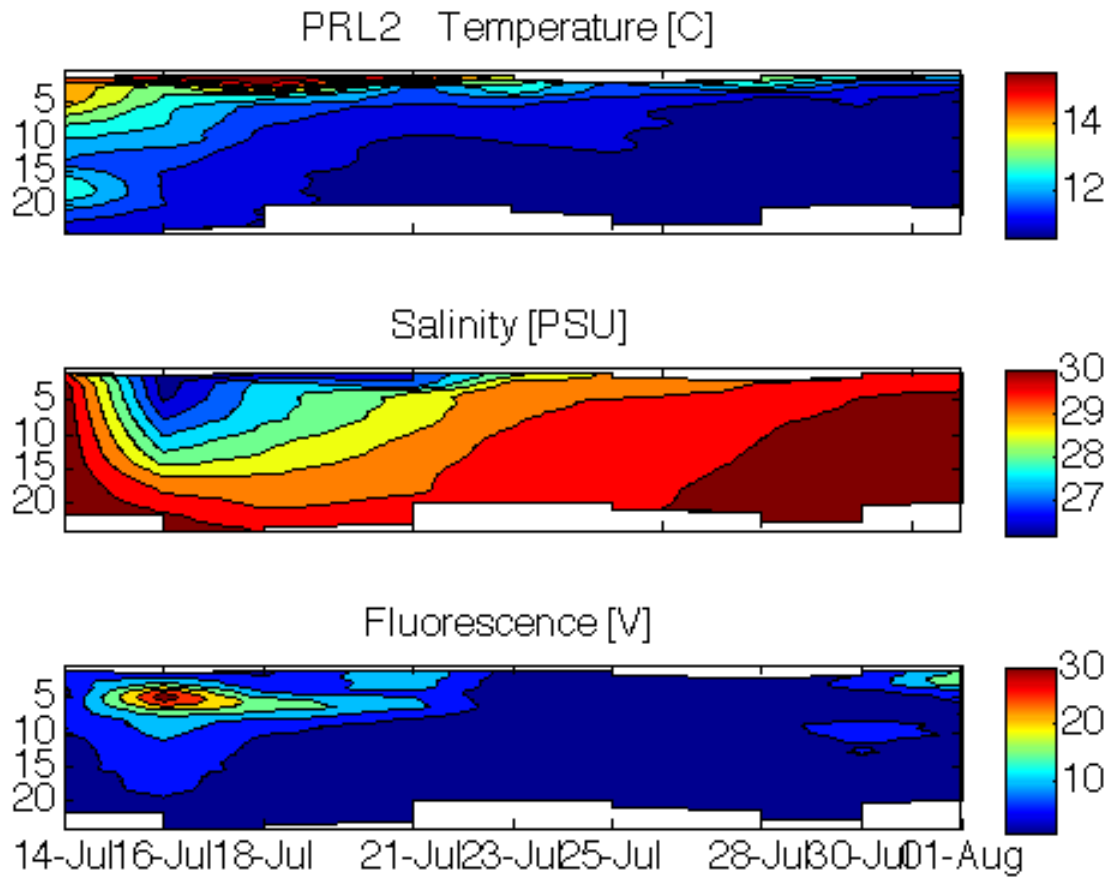


Figure 2 *Interpolated distributions of, from top, temperature (°C), salinity (PSU) and fluorescence (volts) at the southernmost station, just within the fjord (PRL 2) over duration of the field-work. CTD casts were taken on alternating days. Cooling of the water column and an intrusion of lower salinity water can be seen, changing the physical structure of the water column. Biological structure is observed in the form of distinct, subsurface patches of phytoplankton fluorescence.*

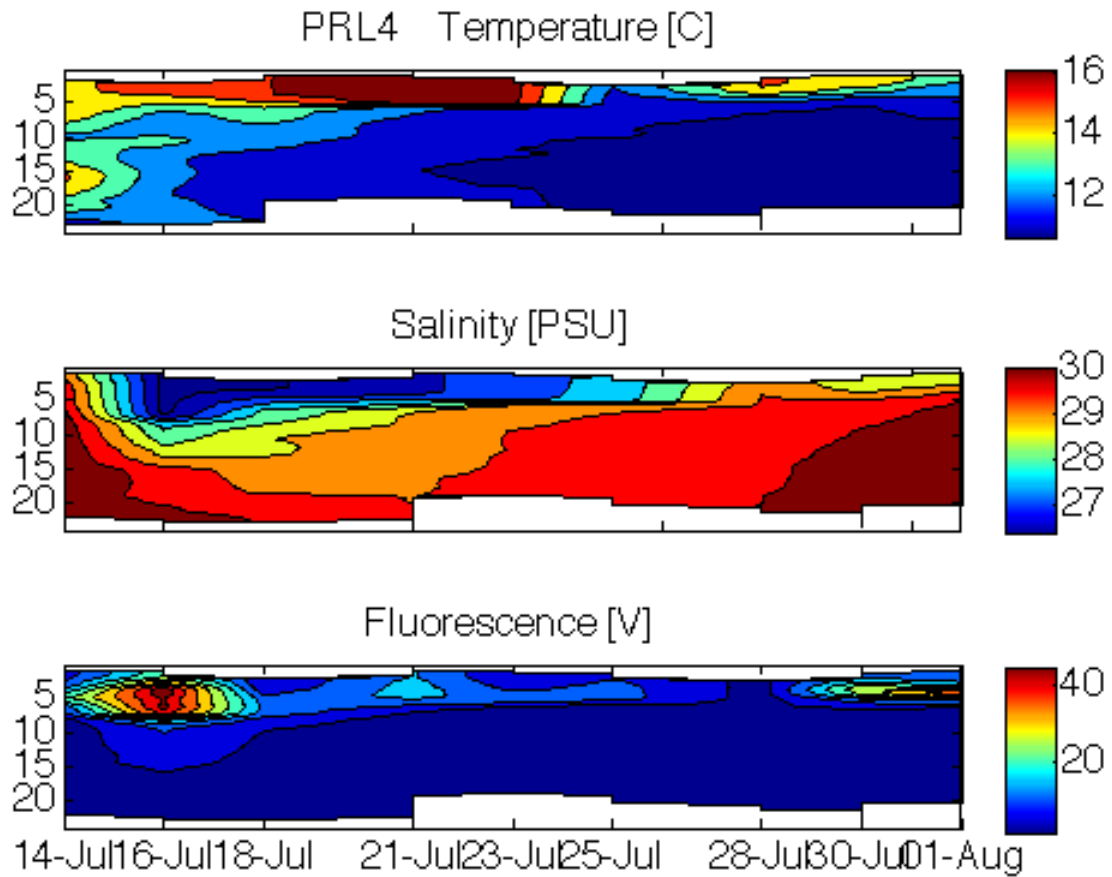


Figure 3 As figure 2 for the northern station (PRL 4). Cooling of the water column is less intense than at the southern terminus of East Sound and the low salinity intrusion persists longer. The intensity of fluorescence patches is much higher than at all other stations.

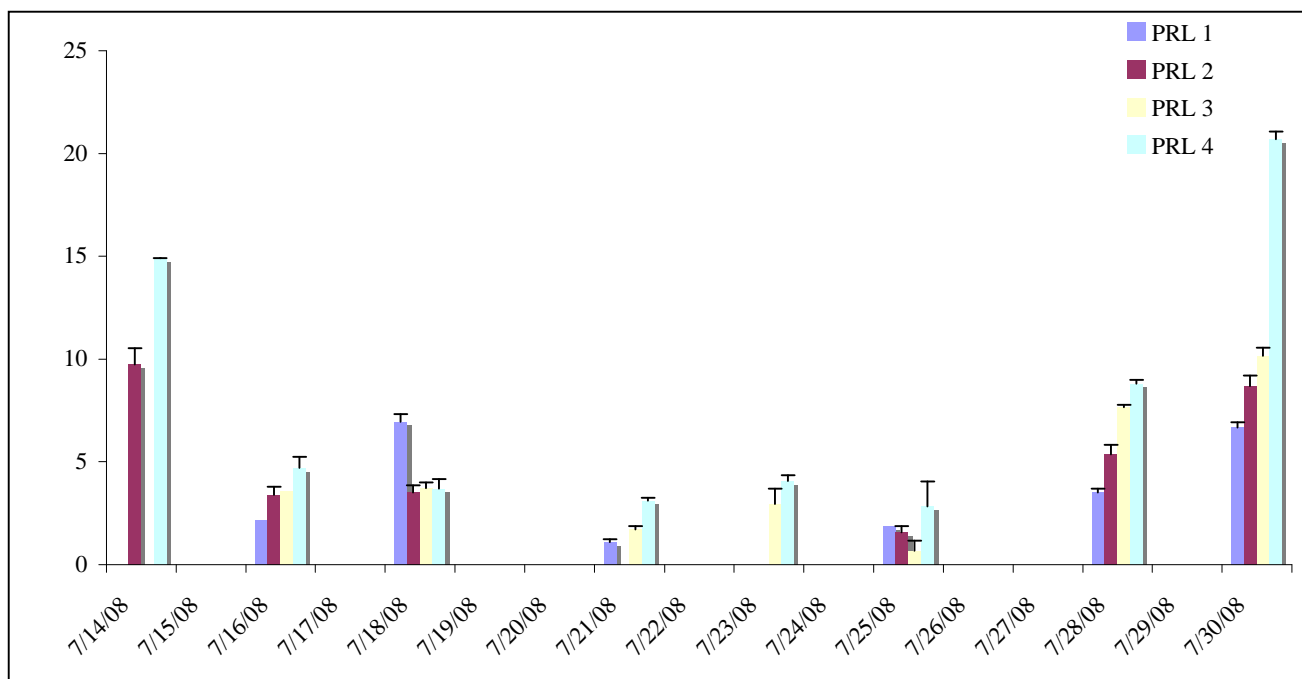


Figure 4 Total Chl a concentration ($\mu\text{gChl a/l}$) over the course of the sampling period at stations PRL 1 to 4, from south to north. Fewer samples were taking during the period July 21 through 24, when phytoplankton abundance was very low. The presence of the initial prasinophyte layer is apparent as well as the development of the diatom layer (July 28 to 30th 2008). As in 2007, total Chl a concentration was highest at the northern station PRL 4.

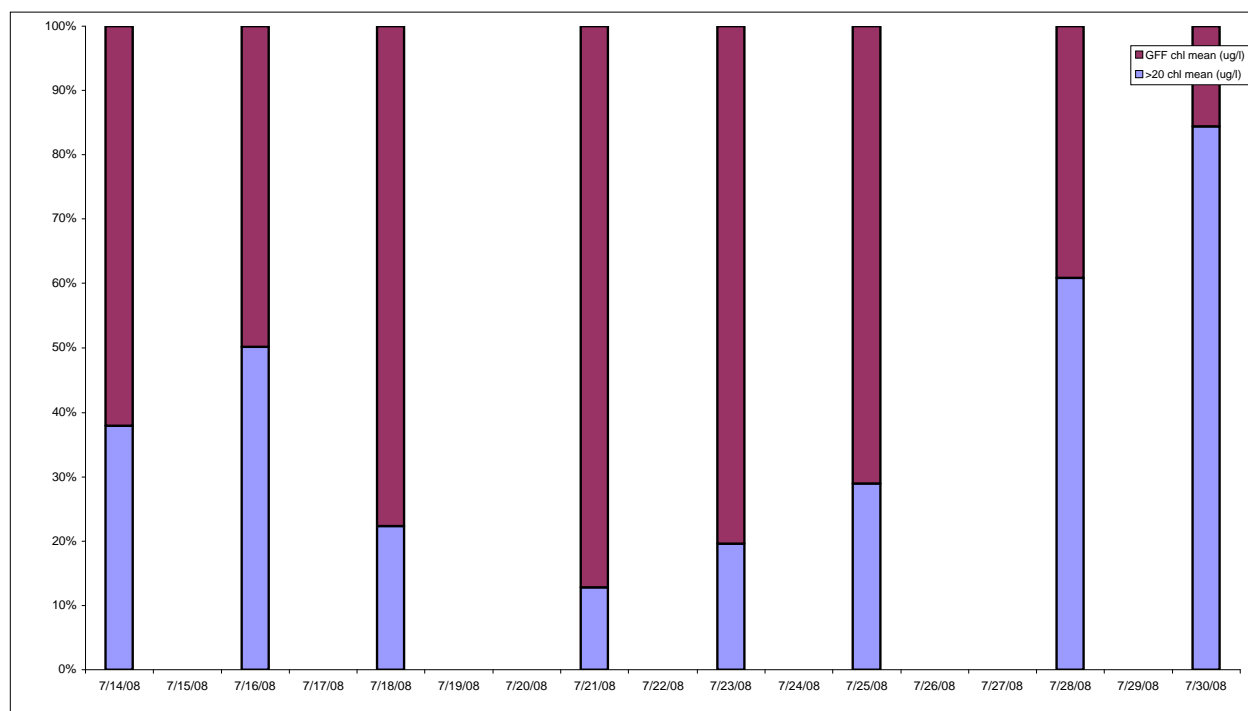


Figure 5 Contribution of the $>20\ \mu\text{m}$ (blue) and $<20\ \mu\text{m}$ (purple) size fraction to total Chl a. The appearance of the diatom-dominated layer at the end of our observation period is apparent.

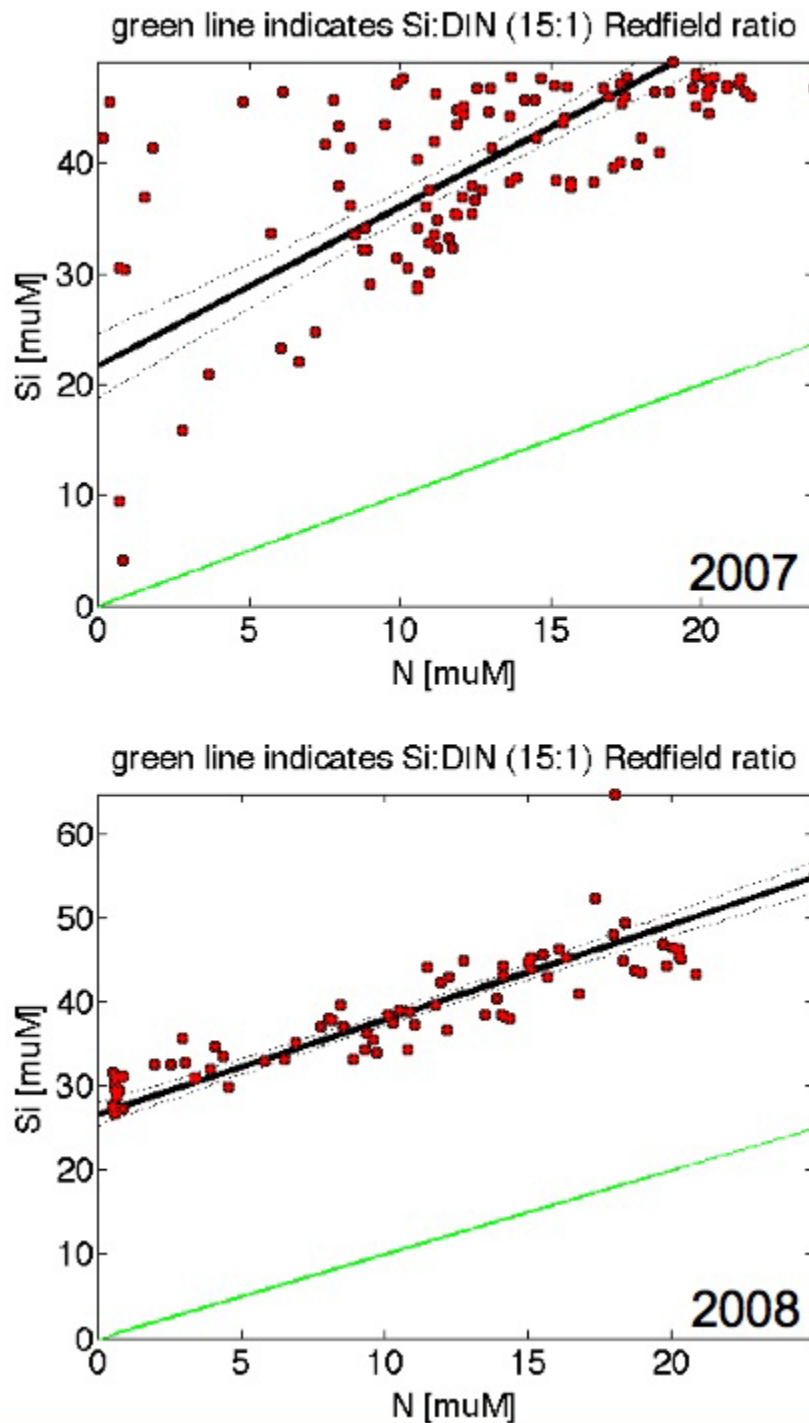


Figure 6 Dissolved inorganic macro-nutrient concentrations where measured inside and outside plankton-rich layers at each station, on each cruise. During both seasons, 2007 and 2008, nutrient concentrations were limiting with respect to Redfield ratios for nitrate and phosphorous. Silicic acid was available in excess. Linear regression analysis confirms that nutrient concentrations are significantly, positively correlated and that availability of nitrate and phosphate is significantly lower than Redfield ratio concentrations.

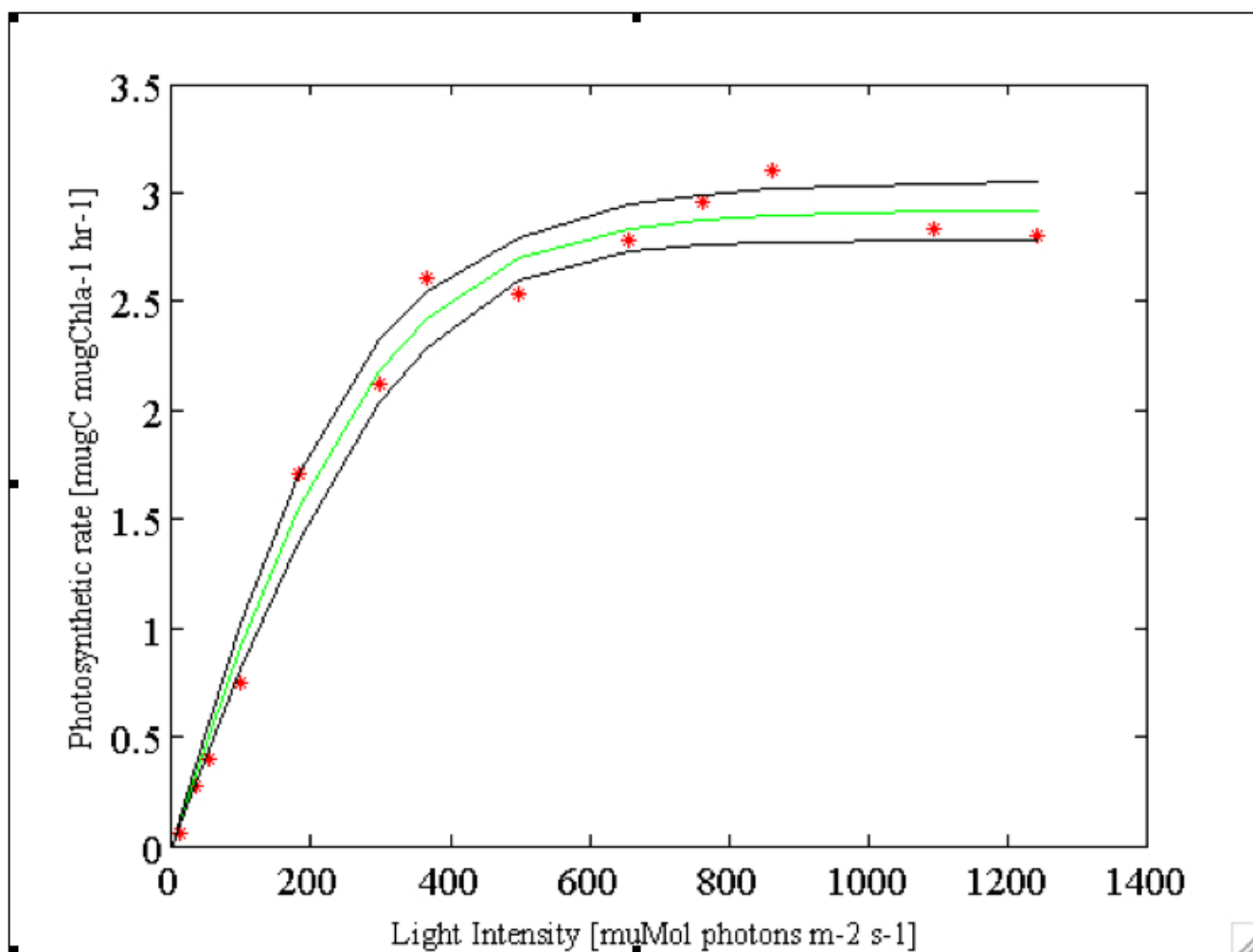


Figure 7 Photosynthesis vs. irradiance curve for whole plankton communities. Non-linear regression analysis provides probability and significance levels for the characteristic parameters, providing a basis for comparing photosynthetic performance of layer and non-layer phytoplankton and thus an analysis of whether growth is a contributing factor in layer formation. The light levels where chosen based on the surface light intensities observed in East Sound in July 2006.